

GEOGRAPHIC VARIATION OF THE NUMBER OF B-CHROMOSOMES IN *METAGAGRELLA TENUIPES* (OPILIONES, PHALANGIIDAE, GAGRELLINAE)

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Chromosomes of *Metagagrella tenuipes* (L. Koch) (Arachnida, Opiliones, Phalangidae, Gagrellinae) were surveyed in 8 populations in Japan. Almost every individual examined had one or more (highest number per cell was 19) supernumerary or B-chromosomes, in addition to the basic set of chromosomes ($2n=18$). These B-chromosomes are heterochromatic, and during meiosis they appear to behave as univalents. The number of B-chromosomes varied both among and within populations. The number also fluctuated to some extent among cells from the same individual, suggesting nondisjunction at mitotic anaphases. No correlation could be elucidated between the number of B-chromosomes and external morphologies or habitat type. The number of B-chromosomes may affect growth rate, and in turn reduce the synchrony of breeding within a population.

Die Chromosomen von *Metagagrella tenuipes* (L. Koch) (Arachnida, Opiliones, Phalangidae, Gagrellinae) wurden in 8 japanischen Populationen untersucht. Fast jedes überprüfte Individuum wies eines oder mehrere (die höchste Anzahl pro Zelle war 19) überzählige oder B-Chromosomen zusätzlich zum Standardchromosomensatz ($2n = 18$) auf. Diese B-Chromosomen sind heterochromatisch und scheinen sich während der Meiose als Univalente zu verhalten. Die Zahl der B-Chromosomen variiert sowohl zwischen als auch innerhalb von Populationen. Sie schwankt in gewissem Ausmaß auch zwischen Zellen aus ein und demselben Individuum, was auf Non-Disjunction bei mitotischen Anaphasen schließen läßt. Zwischen der Anzahl der B-Chromosomen und der äußeren Morphologie oder Habitattypen konnten keine Korrelationen gefunden werden. Es besteht die Möglichkeit, daß die Zahl der B-Chromosomen die Wachstumsrate beeinflussen und in der Folge die Synchronie der Fortpflanzung innerhalb einer Population reduzieren kann. □ *Opiliones, Metagagrella tenuipes, Japan, B-chromosomes, geographic variation.*

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The harvestman *Metagagrella tenuipes* (L. Koch) is widespread throughout Japan but with a peculiar habitat and distribution pattern. In southern Japan, this opilionid is typically coastal. However, in northern Japan, it also occurs inland and prefers open habitats, e.g. parks and gardens, that are affected by moderate human disturbance.

During a chromosomal survey of this species, the number of chromosomes varied both within and among populations, with a range of $2n=18$ to 36. Moreover, the number of chromosomes varied somewhat from one cell to another in almost all individuals. Close examination of mitotic and meiotic chromosomes revealed that the karyotype of this species is usually composed of $2n=18$ standard chromosomes and one or more supernumerary or B-chromosomes, and that the latter cause the overall chromosome number to vary. Here, I will describe the karyotype, nature of the B-chromosomes, and pattern of geographic variation in the B-chromosome number.

MATERIALS AND METHODS

The specimens used for chromosome examination are listed (Table 1, Fig. 1). Cytological data were obtained from air-dried preparations of testes or ovaries of field-collected adults and penultimate instars. The technique used is described in Tsurusaki (1985) and Tsurusaki and Cokendolpher (1990). In some cells, patterns similar to C-bands were observed despite the fact that these cells had received no special treatment. In many individuals the number of B-chromosomes varied from cell to cell. In such cases, the chromosome number of each is represented by a modal number.

For two populations (Nakajima and Maruyama), lengths of femur I of the specimens used in the chromosome preparation were measured with an eyepiece graticule.

Detailed collection data on the specimens examined are listed in the appendix.

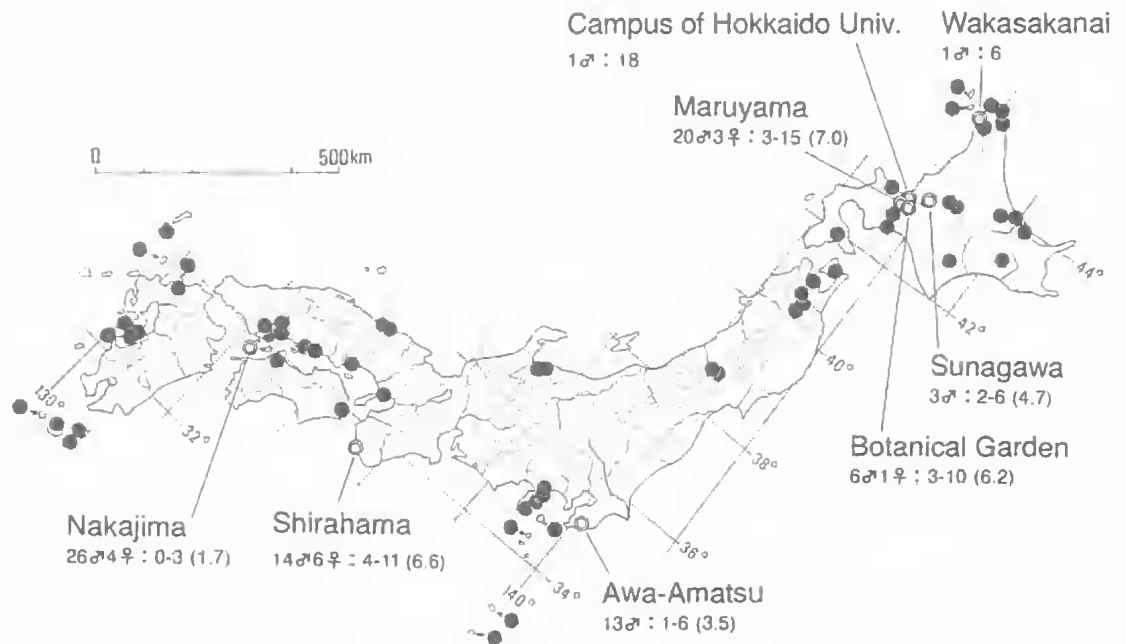


FIG. 1. Map of populations of *M. tenuipes*, Japan, used here (double open circles) with records compiled from literature (e.g. Suzuki, 1973; Suzuki and Tsurusaki, 1983) and data in the appendix (solid circles). No. of samples and range of B-chromosome number in each study population are shown, with means in parentheses.

RESULTS

KARYOTYPES AND NATURE OF B-CHROMOSOMES

The chromosome number of this species varied enormously among and within populations. From comparisons of the karyotypes of individuals with the lowest chromosome number, $2n=18$, to those from others with $2n=19$ and greater, and from analyses of both meiotic chromosomes and unintentionally obtained C-banded chromosomal spreads, the chromosome number of the standard karyotype, which consists of so-called A-chromosomes alone, was determined to be $2n=18$ for both males and females (Figs 2-3).

1. *Standard karyotype* (Fig. 3)

Autosomes consist of 8 pairs of medium-sized metacentrics (Nos. 4 and 5), submetacentrics (Nos. 1, 3, 7, 8), and subtelocentrics (Nos. 2 and 6). The X chromosome, the largest, is subtelocentric, while Y is submetacentric and similar in size to chromosome No. 1. In C-banded mitotic metaphases, centromeric regions of the A-chromosomes were positively stained (Figs 4-5). No prominent differences were found among the

TABLE 1. B-chromosome numbers in 8 populations of *Metagagrella tenuipes*. NOTES: ¹ S = seashore habitats, I = inland habitats e.g. parks, fields; ² Range, mean and mode not for all cells counted but for values represented by mode of each individual; ³ Calculated only for samples with >5 individuals; ⁴ One or more were juveniles.

Locality and habitat type in parentheses ¹	Date	Specimens examined	Number of B-chromosomes ²				
			min.	max.	mean	mode	SD ³
Wakasakanai (S)	9-IX-1985	1 ♂ ⁴	6	6	6	6	-
Sunagawa (I)	8 & 15-X-1986	3 ♂	2	6	4.7	6	-
Campus of Hokkaido Univ. (I)	18-IX-1981	1 ♂	18	18	18	18	-
Botanical Garden, Sapporo 1982 (I)	5-IX-198	5 ♂, 1 ♀	4	10	6.2	4	2.40
as above, 1986 (I)	8-VIII & 9-IX-1986	8 ♂, 2 ♀	3	9	6.2	5, 7, 8	1.93
Maruyama, Sapporo (I)	5-IX-1986	20 ♂, 3 ♀	3	15	7.0	6	2.75
Awa-Amatsu (S)	27-VIII-1984	13 ♂	1	6	3.5	4	1.39
Shirahama (S)	29-VII-1983	14 ♂, 6 ♀ ⁴	4	11	6.6	6	1.60
Nakajima (S)	26-VIII-1986	26 ♂, 4 ♀	0	3	1.7	1, 2	1.02

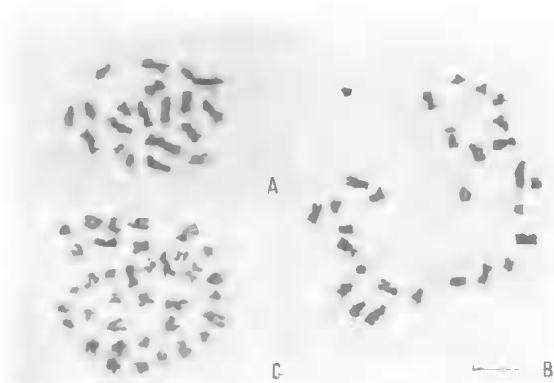


FIG. 2. Representative chromosome complements at spermatogonial mitotic metaphase of male *Metagagrella tenuipes*. A, Nakajima, $2n=18$ (18A's); B, Maruyama, $2n=28$ (18A's + 10B's); C, campus of Hokkaido Univ., $2n=37$ (18A's + 19B's). Scale = $5\mu\text{m}$.

standard karyotypes of individuals from various populations.

2. B-chromosomes

In addition to a set of standard chromosomes described above, almost all chromosomal spreads contained at least one B-chromosome. These were meta- or submetacentric, equal to or smaller than the shortest pairs (No. 8) of the A-complement (Fig. 3). In C-banded chromosome spreads, the B's were heteropycnotic, darkly staining along their total lengths (Figs 4-5). During meiosis, the B's remained univalent (Fig. 4-5) even when the cell carried 2 or more. The number of B's varied considerably from one cell to the other within a single individual, possibly due to nondisjunction at anaphase during mitosis.

Numeric variation in B's among individuals within populations was also evident (Fig. 6). No significant differences were found in the number of B's between the sexes from any population (Mann-Whitney U-tests for each of four populations where both sexes were sampled, $P=0.48-0.96$).

GEOGRAPHIC VARIATION IN NUMBER OF B'S

The number of B-chromosomes varied significantly among populations (single classification ANOVA: $F=34.6$; $d.f.=7$; $P<0.001$) (Figs 1 and 6, Table 1). The lowest and the highest population means of the number of B's were 1.7 for Nakajima ($n=30$) and 18 for the campus of Hokkaido University ($n=1$), respectively, and the means of the other populations lay between the two extremes, range = 3.5-7. However, no significant correlations could be detected between the number of B's and characteristics such as

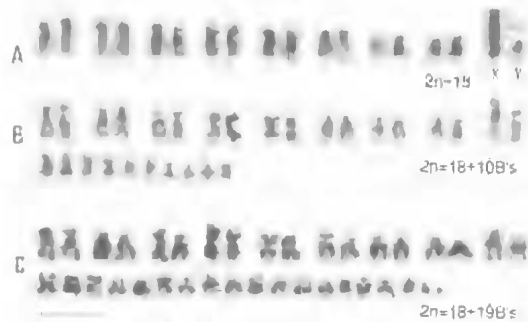


FIG. 3. Karyotypes of male *Metagagrella tenuipes* based on the photographs in Fig. 2. A, Nakajima; B, Maruyama; C, campus of Hokkaido Univ. B-chromosomes are arranged on the second row in B and C. Scale = $5\mu\text{m}$.

latitude (Spearman's coefficient of rank correlation, $r_s=0.19$, $n=8$, $P>0.05$) and habitat types (seashore or inland; Mann-Whitney U-test, $P>0.05$).

DISCUSSION

CHARACTERISTICS OF THE B-CHROMOSOMES

According to Jones and Rees (1982), B-chromosomes have been reported in over 1000 species of plants and more than 260 species of animals. In Arachnida, however, only three species of Acari have been shown to have B's: *Aponomma fimbriatum* and two species of *Haemaphysalis* (Oliver and Bremner, 1968; Oliver *et al.*, 1974).

The B-chromosomes in *Metagagrella tenuipes* have the following characteristics that are typical for B's recorded in various other organisms (White, 1973; Jones and Rees, 1982; Werten *et al.*, 1988; Shaw and Hewitt, 1990; Jones, 1991): (1) they are smaller than most members of the A-complement; (2) they appear to be comprised of a large amount of constitutive heterochromatin; (3) they remain univalent during meiosis; (4) the number of B's varies from one cell to another even within an individual, indicating they display nondisjunction at anaphases of spermatogonial mitoses.

However, the frequency and the number of B's were rather unusual. In this species, every population sampled contained B's and the frequency within a population was up to 87% in Nakajima and 100% in the other 7 populations. The number of B's retained per individual of this species was also extraordinarily high; the population means had a range from 3.5 to 7 in 6 out of 8 populations

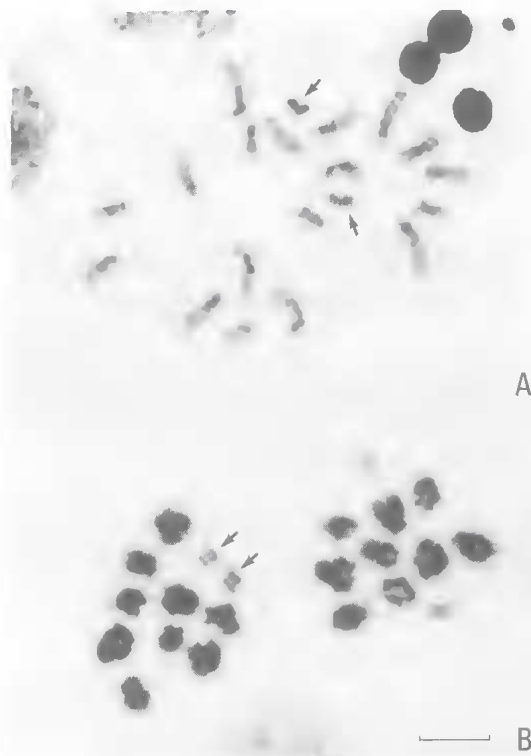


FIG. 4. C-banded mitotic metaphase (A) and meiotic metaphase I (B) in ♂ *M. tenuipes* from Sunagawa, with 2 B-chromosomes (arrowed). Scale = 5 μ m.

(Table 1). The higher end was found in the single male sampled from the campus of Hokkaido University, whose modal number of 18 B's was exhibited by 30 cells and the maximum number of 19 in 3 cells (Figs 2-3). These are among the highest numbers of B's in animal species so far recorded, close to the number 'about 20' in *Xylota nemorum* (Diptera: Syrphidae) (Boyes and Van Brink, 1967).

EFFECT OF B'S ON PHENOTYPE

Metagagrella tenuipes shows marked variation both among and within populations in external morphology, such as body size, leg lengths, degree of development of a spine on the dorsal scutum, number of noduli on the legs, and coloration of the body (Suzuki, 1973; Suzuki and Tsurusaki, 1983). However, no correlation was found between these characters and the number of B-chromosomes (Fig. 7). These facts are consistent with the observation that the B's are C-band positive. If these B's are indeed genetically inactive, numerical variation of B's would lead to no effect on the phenotype of their owner.

Although few studies have demonstrated any

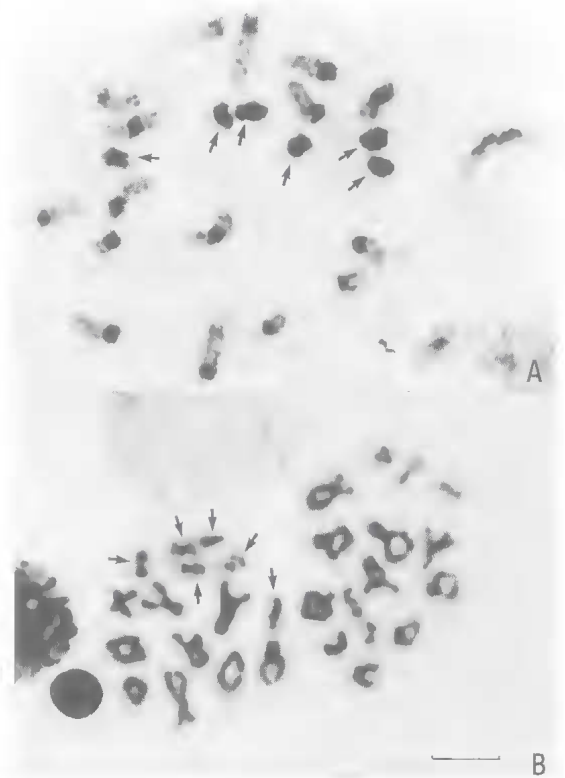


FIG. 5. C-banded mitotic metaphase (A) and diakinesis - metaphase I (B) in ♂ *M. tenuipes* from Maruyama, with 6 B-chromosomes (arrowed). Note: 9 bivalents formed by 9 pairs of A-complement of chromosomes. Scale = 5 μ m.

exophenotypic effect due to B's, some show a relationship between the number of B-chromosomes and the rate of development (Hewitt and East, 1978; Harvey and Hewitt, 1979). Thus, there is a possibility that the presence of B-chromosomes retards the cell cycle due to the additional DNA or its organization which is possibly different from A-chromosomes. In turn, these effects may influence the growth and development of the whole organism (Jones and Rees, 1982). Such influences might be related to an unusual feature of the life history of this species, namely, high variability among individuals in the time to reach maturity. The duration of coexistence of juveniles and adults of this species at Maruyama is estimated to be about three weeks, whereas it is less than 1-2 weeks in other species of opilionids having no B-chromosomes, such as *Oligolophus aspersus*, *Leiobunum japonicum*, and two species of *Nelima* from the same locality (Tsurusaki,

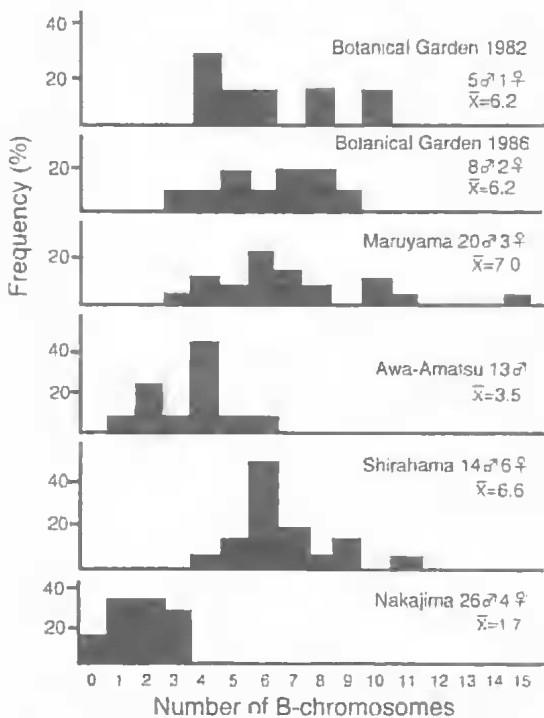


FIG. 6. Frequency distribution of B-chromosome numbers in 6 samples from 5 populations. The other 3 populations (Wakasakanai, Sunagawa, and campus of Hokkaido Univ.) omitted due to paucity of specimens surveyed.

unpublished data based on weekly field-collections made in 1979). The same phenomenon is also inferred from field-data from various localities all over Japan. This versatility in the timing of final molting of this species might be ascribed to the numerical variation of B-chromosomes. Further study is needed.

GEOGRAPHIC VARIATION IN NUMBER OF B'S

The fact that the B's are found in every population over a wide geographic range of this species indicates that they are of rather ancient origin. Marked morphological variation among the B-chromosomes also attests to their long evolutionary history. However, it is also possible that they might be produced *de novo* from the A-complement by recurring mutation.

Although B's appear widespread across the species range, the number of B's considerably varied among populations, with a fairly wide range from 1.7 at Nakajima to 18 on the campus of Hokkaido University. In each population, the number of B's may be stable for at least several years; there was no significant difference in their

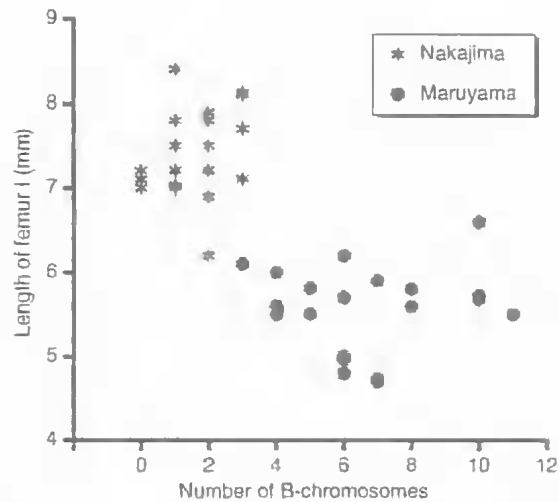


FIG. 7. Relation of length of femur I to number of B-chromosomes in 2 populations (Nakajima and Maruyama) of *M. tenuipes*. No significant correlation between 2 variables in each population [$r = 0.305$ ($P > 0.1$) for Nakajima; $r = 0.065$ ($P > 0.1$) for Maruyama], although both characters show prominent differences between two populations. Two variables may be negatively correlated (although spuriously) between populations. Leg lengths decrease with increase in latitude (Tsurusaki, unpubl.) but the number of B's does not.

frequencies in the Botanical Garden at Sapporo which were sampled in 1982 and 1986 (Fig. 6). If B-chromosomes were inherited in a non-Mendelian manner, and were neutral in phenotypic expression, the frequency of B's would not be stable. For example, it might be expected that the crossing of a male with 3 B's and a female with 3 B's would produce some offspring with 4 or more B's. However, no individuals with more than 3 B's are found in Nakajima population. This indicates that some selection pressure limits the number of B's that one individual can retain in a particular population. It is still uncertain what factors determine the population mean and the range of the number of B's. However, this species may be useful in studying various aspects of B's and 'selfish' DNA, including the controversial issues on the level of selection discussed by Werren *et al.* (1988) and Shaw and Hewitt (1990).

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APPENDIX. New material of *M. tenuipes* used in Fig. 1. Data in order: locality, altitude if available and needed, no. individuals, no. specimens dissected in parentheses if needed (Value may not be as in Table 1, since no countable chromosomal spreads were obtained for some specimens), date collected, collector (NT = N. Tsurusaki; YN = Y. Nishikawa).

HOKKAIDO: I. Rebun, Kabukai, Kabukai Elementary School, 10m, 1 juv., 11-viii-1990, YN. I. Rishiri: Oshidomari, ca. 20m, 1 ♂, 8-viii-1985, Y. Kuwahara; Oshidomari, 5m, 1 ♀, 2 juv., 7-9-viii-1990, S. Ueno, M. Sato, YN; Fujino, 10m, 1 juv., 7-viii-1985, NT. Wakkanai: Soya Point, 1m, 2 ♂, 3 ♀, 1 juv., 2-ix-1988, NT; Wakkanai Port, 2m, 4 ♀, 5 juv., 7-viii-1985, S. Ishimaru, NT. Esashi-gun: Hamatonbetsu-chō, Beniya-Genseikaen, 2 ♂, 1 ♀, 8 juv., 14-15-viii-1990, YN. S. Ueno. Teshio-gun: Toyotomi-chō, Wakasakanai, on coastal sand dune: 1 juv. (1 juv.), 9-viii-1985, NT; 1 ♂, 1 ♀, 1-ix-1988, NT. T. Tanabe. Toyotomi-chō, Toyotomi Spa, 2 ♂, 1 ♀, 1 juv., 12-13-viii-1990, YN. Monbetsu-gun, Engaru-chō, Engaru JR Station, 2 juv., 30-vi-1985, NT. Kantikawa-gun, Tōma-chō, Tōma Cave, outside cave, 4 ♀, 29-30-viii-1985, N. Yoshida. Sunagawa, On a bank of R. Penke-Utashinai, 1 ♂ (1 ♂), 8-x-1986; 2 ♂ (2 ♂), 15-x-1986, NT. Sapporo: campus of Hokkaido Univ., 1 ♂, 1 ♀, 18-ix-1981, NT; Botanical Garden of Hokkaido Univ.: 9 ♂, 9 ♀ (5 ♂, 1 ♀), 5-ix-1982, NT; 13 ♂, 16 ♀, 5-ix-1984; 7 juv. (7 juv.), 8-viii-1986; 3 ♂ (3 ♂), 9-ix-1986, NT. Sapporo, Maruyama, 23 ♂, 19 ♀ (20 ♂, 3 ♀), 5-ix-1986, NT. Tomakomai, Tomakomai Experiment Forest of Hokkaido Univ., 1 ♂, 3 ♀, 19-ix-1980, NT. YAMAGATA PREF.: Obanazawa-shi, Obanazawa, 1 ♂, 1 ♀, 4 juv., 29-viii-1983, A. Otaka; 6 ♂, 1 ♀, 4-x-1984, A. Otaka; Obanazawa-shi, along Route 347, 2 ♀, 9-x-1988, T. Tanabe. CHIBA PREF.: Awa-gun, Amatsu-Kominato-chō, Awa-Amatsu, Saneiri coast: 1 ♂, 1 ♀, 2 juv., 21-v-1983; 1 ♂, 18-ix-1983, K. Ishii; 2 ♂, 1 ♀, 18-xii-1983, K. Ishii. Awa-Amatsu, Saneiri, Matsugabana, under growth of maritime fern, *Cyrtomium falcatum*, 1-2m, 23 ♂, 21 ♀ (16 ♂), 27-viii-1984, NT. TOKYO PREF.: I. Hachijo, Mine, 2 ♂, 2 ♀, 17-18-xi-1983, H. Okada. TOYAMA PREF.: Toyama-shi: Yokogoshi, 1 ♀, 20-x-1978; 1 juv., 18-v-1990, N. Nunomura; Hamakurosaki, *Pinus thunbergi* forest, 1 juv., 2-v-1979; 3 ♂, 1 ♀, 6-viii-1980, N. Nunomura. WAKAYAMA PREF.: Nishimuro-gun, Shirahama-chō, Shirahama, Seto Marine Biological Lab., 1 ♂, 3 ♀, 10-vii-1983, S. Otsuka; 29 ♂, 41 ♀, 43 juv. (16 ♂, 1 ♀, 9 juv.), 29-vii-1983, NT. TOTTORI PREF.: Iwami-gun, Iwami-chō, Uradome coast, Kamogaiso, 4 ♂, 3 ♀, 7-ix-1988, NT, R. G. Holmberg; Ketaka-gun, Ketaka-chō, Yatsukami, Anedomari coast, 1 ♂, 3 ♀, 5-ix-1987, NT. OKAYAMA PREF.: Oku-gun, Ushimado-chō, Ushimado Marine Biological Station of Okayama Univ., Benten-iwa, 1 ♂, 4 ♀, 10-viii-1983, T. Sato. HIROSHIMA PREF.: I. Nōmi-jima, Irukanohana: 12 juv., 13-vi-1976; 1 ♂, 4-vii-1977, NT. EHIME PREF.: Onsen-gun, Nakajima-chō, I. Nakajima, Okushi: 3 ♀, 6-7-viii-1971; 1 ♀, 13-viii-1974, NT; Okushi, Seno-hana, 51 ♂, 69 ♀ (30 ♂, 6 ♀), 26-vii-1986, NT. I. Nakajima: Himegahama, 1 ♀, 13-viii-1974, NT; I. Takashima off Himegahama, 3 ♂, 3 ♀, 6-viii-1971, NT. Matsuyama, Mt. Fukumi, Fukumiji, 860m, 2 juv., 6-ix-1970, NT. NAGASAKI PREF.: Iki-gun, Ishida-chō, Kukishoku, 4 ♂, 5 ♀, 2 juv., 20-vi-1990, M. Yamashita. KUMAMOTO PREF.: Ushibuka-shi, I. Tojima, 2 juv. M. Yoshikura; Amakusa-gun, Itsuwa-chō, Oniike, 3 ♂, 1 ♀, 2 juv., 8-vii-1958, M. Yoshikura; Matsushima-chō, Aitsu, 4 ♂, 1 ♀, 10-viii-1957 M. Yoshikura; Matsushima-chō, I. Macjima, 2 ♂, 4 ♀, 20-vii-1963, M. Yoshikura. KAGOSHIMA PREF.: I. Yakushima, Shiratani-Unsui-kyō to Mt. Miyanoura-dake, 1 ♀, 2-5-viii-1983, H. Okada. I. Tanegashima: Hamada, 1 juv., 11-vii-1983, Sk. Yamane; Makigawa, 3 juv., 3-5-v-1984, Sk. Yamane. Kumage-gun, Kamiyaku-chō, I. Kuchinoerabu-jima, 1 ♂, 27-iv-1984, Collector unknown.